Natal homing in juvenile loggerhead turtles (*Caretta caretta*)

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Abstract

Juvenile loggerhead turtles (*Caretta caretta*) from West Atlantic nesting beaches occupy oceanic (pelagic) habitats in the eastern Atlantic and Mediterranean, whereas larger juvenile turtles occupy shallow (neritic) habitats along the continental coastline of North America. Hence the switch from oceanic to neritic stage can involve a trans-oceanic migration. Several researchers have suggested that at the end of the oceanic phase, juveniles are homing to feeding habitats in the vicinity of their natal rookery. To test the hypothesis of juvenile homing behaviour, we surveyed 10 juvenile feeding zones across the eastern USA with mitochondrial DNA control region sequences ($N = 1437$) and compared these samples to potential source (nesting) populations in the Atlantic Ocean and Mediterranean Sea ($N = 465$). The results indicated a shallow, but significant, population structure of neritic juveniles ($\Phi_{ST} = 0.0088$, $P = 0.016$), and haplotype frequency differences were significantly correlated between coastal feeding populations and adjacent nesting populations (Mantel test $R^2 = 0.52$, $P = 0.001$). Mixed stock analyses (using a Bayesian algorithm) indicated that juveniles occurred at elevated frequency in the vicinity of their natal rookery. Hence, all lines of evidence supported the hypothesis of juvenile homing in loggerhead turtles. While not as precise as the homing of breeding adults, this behaviour nonetheless places juvenile turtles in the vicinity of their natal nesting colonies. Some of the coastal hazards that affect declining nesting populations may also affect the next generation of turtles feeding in nearby habitats.

Keywords: Bayesian, conservation genetics, marine turtles, mitochondrial DNA, mixed stock analysis

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Introduction

Loggerhead turtles have two distinct juvenile stages, the first being an oceanic stage after hatching (Carr 1987; Bolten

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2003a). For posthatchling turtles departing the nesting beaches of the western Atlantic, this oceanic habitat includes waters around the Azores and Madeira, and the Grand Banks (Newfoundland, Canada), as well as the Mediterranean Sea (Bolten *et al.* 1998; Laurent *et al.* 1998; Bolten 2003a; LaCassella *et al.* 2004). Subsequent to the oceanic stage, which may span a decade (Bjorndal *et al.* 2000, 2003), most older

juveniles enter a neritic (benthic feeding) stage, in which they consume hard-shelled invertebrates in shallow habitats of the western Atlantic (Dodd 1988; Bolten 2003b). Whereas the journey from nesting beaches to oceanic juvenile habitat is largely mediated by passive transport, the return trip may include active orientation and swimming (Bolten 2003a).

Upon reaching sexual maturity, female loggerheads make reproductive migrations to breed and nest in the vicinity of their natal beach (Bowen *et al.* 1993). Male loggerheads may make a similar migration to breeding areas near their natal beach (see FitzSimmons *et al.* 1997a,b). Hence homing behaviour is widely accepted for the reproductive migrations of adults. This raises the question of whether juveniles also exhibit homing behaviour during their trans-oceanic migration. Genetic markers hold considerable promise for addressing this issue. As a consequence of natal homing by females, most nesting populations are distinguished by differences in the frequency of mitochondrial DNA (mtDNA) haplotypes (Bowen *et al.* 1994; Encalada *et al.* 1998; Hatase *et al.* 2002a). It is possible to use these natural genetic 'tags' to resolve the origin of feeding populations, even when the feeding population is a mixture of turtles from several source nesting populations (Bowen 1995, 2003). Mixed stock analyses have been used to monitor salmon for over 20 years (Grant *et al.* 1980), but this methodology has seldom been applied to other organisms (Broderick *et al.* 1994; Epifanio *et al.* 1995; Wirgin *et al.* 1997).

Previous mtDNA studies by Norrgard & Graves (1996), Rankin-Baransky *et al.* (2001), Witzell *et al.* (2002), Engstrom *et al.* (2002) and Bass *et al.* (2004) concluded that contributions to juvenile loggerhead habitats are influenced by the size of regional source (nesting) populations. The very large rookery in southern Florida contributes most of the neritic-stage turtles feeding along this coast, with smaller but significant contributions from the rookeries on the Yucatan peninsula, Gulf of Mexico, and the Atlantic states of Georgia, South Carolina and North Carolina. The same mtDNA studies prompted authors to suggest that juvenile turtles may tend to feed in the vicinity of their natal nesting colony. Hence, two factors have been postulated to explain the composition of juvenile loggerhead feeding populations: size of source populations and proximity to these sources. A third factor, male-biased dispersal, has been proposed for loggerhead juveniles in the Mediterranean (Casale *et al.* 2002).

These mtDNA surveys invoke the possibility that loggerhead turtles have two distinct homing migrations: the well-known reproductive migration, that brings adults back to their ancestral breeding areas, plus a juvenile migration that brings oceanic migrants to neritic feeding habitats near their location of origin. If juvenile homing occurs in the northwestern Atlantic, how precise is this behaviour? Do older juvenile turtles return to a broad region of the western Atlantic, or do they tend to recruit to feeding grounds near their rookery of origin? The latter possibility
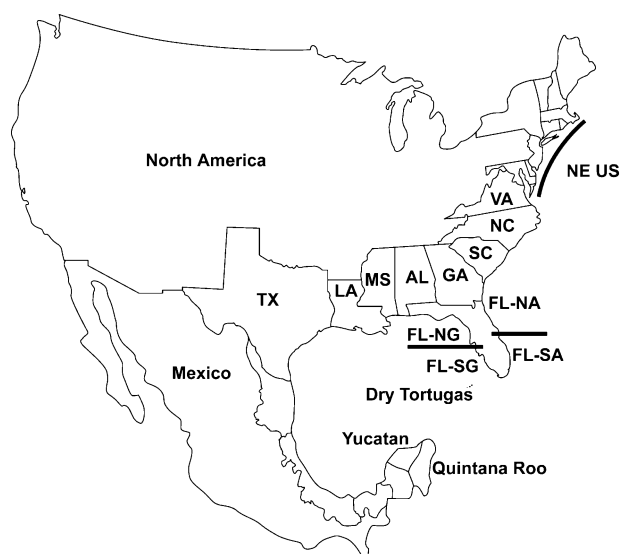

Fig. 1 Map indicating the location of sampled rookeries and foraging grounds in North America. For abbreviations see Tables 1 and 2. Divisions between FL-NA and FL-SA and between FL-NG and FL-SG are indicated by dark bars at Cape Canaveral and Tampa Bay, respectively.

(homing towards natal location) would carry the expectation of population genetic differences among regional feeding cohorts, in parallel with the genetic differences observed between nesting populations (Bowen *et al.* 1993). Previous studies invoked the possibility of juvenile homing (Norrgard & Graves 1996; Rankin-Baransky *et al.* 2001; Engstrom *et al.* 2002; Witzell *et al.* 2002). However, all of these surveys examined a single feeding habitat. To evaluate the veracity and precision of homing, samples from multiple feeding locations across the western Atlantic are necessary.

Here we survey the mtDNA control region sequences of 1437 neritic-feeding individuals (strandings and live captures) along the Atlantic coast of North America from Texas to New England (Fig. 1). We incorporate three previous surveys of juveniles from this region (Rankin-Baransky *et al.* 2001; Witzell *et al.* 2002; Bass *et al.* 2004) along with complementary surveys of regional nesting females (Encalada *et al.* 1998; Laurent *et al.* 1998; Pearce 2001) to resolve the origin of neritic-feeding loggerhead populations and to assess the site fidelity of juveniles. This survey is intended to resolve a gap in loggerhead life history, but the information is relevant to conservation strategies, as thousands of juvenile loggerhead turtles are caught in fishing gear and dredging operations. Wildlife managers need to know which breeding populations are affected by these activities.

Materials and methods

Nest samples had been previously collected from 465 females or progeny from Quintana Roo (Yucatan Peninsula, Mexico),

Table 1 Nesting (source) populations in the Atlantic and Mediterranean, as described in Laurent *et al*. (1998), Pearce (2001) with additional specimens from Encalada *et al*. (1998)

Haplotype	FL-NG	FL-SG	FL-SA	FL-NA	GA	SC	NC	DT	MX	BR	GR	TR
CC-A1	38	20	32	14	42	20	28	4				
CC-A2	7	17	28		1			50	11		78	19
CC-A3	2	4							2			13
CC-A4										11		
CC-A5			1									
CC-A6											2	
CC-A7	2	2	1									
CC-A8									1			
CC-A9								2	1			
CC-A10								2	5		1	
CC-A11			1									
CC-A13												
CC-A14		1	1									
CC-A20		1										
Total	49	45	64	14	43	20	28	58	20	11	81	32

Haplotypes described previously as 'A' through 'Q' have been renamed CC-A1 to CC-A17. Full sequences and haplotype designations are available at http://accstr.ufl.edu/ccmtdna.html. Abbreviations: FL-NG = Florida Peninsula, northern Gulf of Mexico; FL-SG = Florida Peninsula, southern Gulf of Mexico; FL-SA = Florida Peninsula, southern Atlantic coast; FL-NA = Florida Peninsula, northern Atlantic coast (Amelia Island and Jacksonville County); GA = Georgia; SC = South Carolina; NC = North Carolina; DT = Dry Tortugas; MX = Quintana Roo, Mexico; BR = Bahia, Brazil; GR = Kiparissia Bay, Greece and adjacent regions; TR = Turkey.

Bahia (Brazil), Kiparissia Bay (Greece), Turkey and the southeast USA during between 1987 and 1999 (Table 1; for details consult Bowen *et al*. 1993; Encalada *et al*. 1998; Laurent *et al*. 1998; Pearce 2001). Tissue samples (typically an egg or moribund hatchling) were the primary DNA source prior to 1993, and blood samples from nesting females (usually less than 1 ml) were taken in most collections after 1993, following the procedure of Owens & Ruiz (1980) and FitzSimmons *et al*. (1999). Precautions to ensure that nesting females were sampled only once included either (i) tagging the nesting females, or (ii) sampling within a single 11-day interval. Females may nest several times in a nesting season, but rarely at intervals shorter than 11 days (Dodd 1988).

Samples of the feeding populations ($n = 1437$) were collected between 1995 and 2001 (Table 2). Most samples were collected as tissue specimens from stranded individuals (dead and moribund turtles that wash ashore), and these are assumed to represent the local juvenile cohort (Epperly *et al*. 1996). Blood samples were collected from live individuals in North Carolina (Bass *et al*. 2004), and most of the specimens from southeast Florida were collected in a power-plant entrapment system ($n = 106$; Witzell *et al*. 2002). Tissue specimens were stored in a saturated salt buffer (Seutin *et al*. 1991; Dutton & Balazs 1996). This solution is useful for storing specimens at room temperature for at least 5 years.

Size class information was not available in all cases, but the vast majority of specimens came from neritic-stage juveniles in the size range of 40–80 cm straight carapace length. Epperly *et al*. (1995) noted that the habitats sampled here contain few adults. However, we did not conduct internal examination of gonads, so cannot rule out the possibility that a few adults were included in our neritic-stage samples.

Genomic DNA was isolated using a phenol/chloroform procedure followed by ethanol precipitation (Hillis *et al*. 1996). A 391-base-pair (bp) fragment located in the control region of the mitochondrial genome was amplified with polymerase chain reaction (PCR) methodology (Mullis & Faloona 1987), using the primers TCR-5 (5'-TTG TAC ATC TAC TTA TTT ACC AC-3') and TCR-6 (5'-GTA CGT ACA AGT AAA ACT ACC GTA TGC C-3') (Norman *et al*. 1994). For some of the samples a 480-bp fragment of the control region was amplified with LTCM1 and HTCM1 primers from Allard *et al*. (1994). The PCR used standard conditions (Encalada *et al*. 1998) with an annealing temperature of 52 °C and a MgCl$_2$ concentration of 1.5 mM in 50-μL volume reactions. PCR amplifications included negative (DNA free) control reactions to guard against contamination. PCR products were purified using 30 000 MW filter units (Millipore, Inc.). Cycle sequencing reactions were conducted with fluorescent dye-primer and dye-terminator technology (Applied Biosystems Inc.) and fragments were separated on gels at the University of Florida DNA Sequencing Core using an automated sequencer (Applied Biosystems Inc. model 373A or 377), and at the NOAA-Fisheries Molecular Genetics Laboratory at the Southwest

Table 2 Juvenile feeding populations, from biopsies in North Carolina, power plant entrapment system (*n* = 106) and strandings on the coast of southern Florida, and strandings from everywhere else, as described in Rankin-Baransky *et al.* (2001), and Witzell *et al.* (2002)

Haplotype	TX	FL-NG	FL-SG	FL-SA	FL-NA	GA	SC	NC	VA	NE-US
CC-A1	67	10	14	59	37	107	49	166	143	90
CC-A2	53	6	21	58	28	68	32	98	91	53
CC-A3	10	1	5	10	1	10	5	8	4	9
CC-A4								1		
CC-A5						2	1	3	1	1
CC-A6										
CC-A7	4			2		3	2	5	4	1
CC-A8		1		1			1	1		
CC-A9				4	1			1		
CC-A10	2		1	2		2	2	4	3	4
CC-A11				1		1				
CC-A13	1		2	1		2		1	2	
CC-A14	5			6	1	10	3	7	4	3
CC-A18								1		
CC-A19						1				
CC-A20			2	2	1	1			4	
CC-A22						1				
CC-A23						1				
Total	142	18	45	146	69	209	95	296	256	161

Full sequence descriptions are available from http://accstr.ufl.edu/ccmtdna.html. Abbreviations: TX = Texas; FL-NG = Florida Peninsula, northern Gulf of Mexico; FL-SG = Florida Peninsula, southern Gulf of Mexico; FL-SA = Florida Peninsula, southern Atlantic coast; FL-NA = Florida Peninsula, northern Atlantic coast; GA = Georgia; SC = South Carolina; NC = North Carolina; VA = Virginia; NE-US = northeast USA including Maryland, Delaware, New Jersey, New York and Massachusetts.

Fisheries Science Center in La Jolla, CA (Applied Biosystems Inc. models 377 and 3100). Chromatograms were aligned using SEQUENCHER 3.1 (Gene Codes, Inc.). These sequences were compared to previously identified haplotypes from nesting and foraging locations (Bolten *et al.* 1998; Encalada *et al.* 1998) and were assigned haplotype numbers based on the web site maintained by the Archie Carr Center for Sea Turtle Research (http://accstr.ufl.edu/ccmtdna.html).

The mtDNA diversity among populations was measured with an analysis of molecular variance (AMOVA) as implemented in ARLEQUIN version 2.0 (Schneider *et al.* 2000). The same software package was used to conduct a Mantel test and to estimate haplotype diversity, nucleotide diversity and haplotype frequencies (Nei 1987; Excoffier & Slatkin 1995). In all tests that required estimates of sequence divergence, the Tamura–Nei model of nucleotide substitutions was employed (Tamura & Nei 1993). The Mantel test is a comparison of genetic differentiation (Φ_{ST} values) among seven nesting colonies (FL-NG, FL-SG, FL-SA, FL-NA, GA, SC, NC in Table 1) along the continental coast of North America (*X*-matrix), and seven proximal feeding zones (*Y*-matrix). The correlation between these two matrices was evaluated with a permutation test as described by Smouse *et al.* (1986). In a related test, the frequency of the most common haplotype (CC-A1) was compared between seven nesting areas and adjacent feeding populations, calculating the standard Pearson coefficient of determination (R^2) and using a permutation test (with 30 000 permutations) to calculate two-tailed significance against a null hypothesis of $R^2 = 0$.

The availability of data from multiple mixed stocks (feeding populations) and multiple sources (nesting areas), as well as the need to account for the effects of population size, has led us to develop a variation of standard Bayesian methods for mixed stock analysis (see Pella & Masuda 2001; Bolker *et al.* 2003; Bass *et al.* 2004; Okuyama & Bolker 2005). Mixed stock analysis normally estimates the proportion of individuals in a single mixed stock contributed by each of a number of source populations. In the current analysis, where we had multiple sources and multiple mixed stocks, we computed the same parameters—the proportion of each mixed stock contributed by each rookery—but we were also interested in partitioning the other way, finding the fractions of the total contribution to the northwest Atlantic (from each source population) that were present in each mixed stock. In particular, we wanted to know if rookeries contributed disproportionately to nearby feeding populations. Estimating contributions to foraging grounds separately also assumed that all foraging grounds were the same size. Even if we could say that 57% of the feeding individuals in the northeast USA and 69% of those

in South Florida originated from the South Florida rookery, we could not necessarily infer that more turtles from South Florida go to the South Florida foraging ground, if the northern foraging ground had a larger population. Our new method did not make this assumption.

We can estimate these parameters in a straightforward way, if we know the relative sizes of the rookeries and if we make the assumption that the total contributions of nesting populations to the combined feeding populations are proportional to their size. Essentially, if the relative sizes (and therefore overall proportional contributions) of the rookeries are known, we can derive an equation to translate between the partitioning of mixed-stock turtles according to their nesting population of origin and the partitioning of nesting population turtles according to their mixed-stock destination (Bolker *et al.* unpublished results). This procedure can then be incorporated into standard mixed-stock estimation procedures, either in a maximum-likelihood or in a Bayesian estimation framework; we have chosen a Bayesian framework because of its more accurate calculation of confidence limits (Bolker *et al.* 2003). We can examine the estimates from this procedure either in the traditional way, as the fractions of each mixed stock estimated to come from each source population (rookery), or, in the new way, as the fractions of the total contribution from each rookery estimated to be present in each mixed stock. The new method also adds an 'unknown' category to the list of mixed stocks, to allow for the possibility that some of the sampled rookeries contribute to one or more unknown mixed stocks.

Designation of source populations for mixed stock analyses

Based on the population subdivisions defined by Encalada *et al.* (1998), Laurent *et al.* (1998) and Pearce (2001), the nesting samples (Table 1) were grouped into the following source populations for mixed stock analysis: (i) Florida coast in the northern Gulf of Mexico (FL-NG: *n* = 49); (ii) South Florida (SFL, *n* = 109) combining southern Atlantic and southern Gulf coasts of Florida (FL-SA and FL-SG in Table 1); (iii) northeast Florida to North Carolina (NEFL-NC; *n* = 105), combining northern Atlantic coast of Florida, Georgia, South Carolina and North Carolina (FL-NA, GA, SC, and NC in Table 1); (iv) Dry Tortugas, FL (DT, *n* = 58); (v) Quintana Roo, Yucatan, Mexico (MX, *n* = 20); (vi) Bahia, Brazil (BR, *n* = 11); (vii) Greece (GR, *n* = 81); and (viii) Turkey (TU; *n* = 32). These groupings are based on statistically significant differences in haplotype frequencies. Additional population subdivisions almost certainly exist but cannot be detected with the available mtDNA sequence information.

Designation of feeding populations for mixed stock analysis

Juvenile populations from Texas to the northeast USA (Table 2) were analysed without modification for indices

of genetic diversity, haplotype frequency comparisons, *F* statistics, correlation coefficients and the Mantel test. Because of the relatively sparse data from the mixed stocks, analysing the contributions to the mixed stocks in their fully disaggregated form led to very wide confidence limits. We estimated the contributions to each of 11 'foraging grounds' (the 10 foraging grounds represented by the different data sets in Table 2 plus an unknown foraging ground) separately, but we also placed the results into four groups representing a northern mixed stock (N: FL-NA, GA, SC, NC, VA, NEUS in Table 2), a southern mixed stock (S: FL-SA in Table 2), a Gulf of Mexico mixed stock (G: TX, FL-NG, FL-SG in Table 2) and an unknown mixed stock (not shown). As well as considering the basic estimate of contribution to each of the known mixed stocks, we also considered the ratio of the contributions to the total contributions to known stocks [e.g. $N/(N + S + G)$ would represent the contribution to the Northern stock relative to the combined total of Northern, Southern and Gulf contributions]. In addition, we discard 'orphan' haplotypes, the haplotypes from the feeding grounds that were not detected in nesting populations (haplotypes CC-A18, -19, -22 and -23 in Table 2); these specimens provided no additional information about the contributions of nesting populations to feeding grounds. The individuals with 'orphan' haplotypes (*n* = 4) comprised less than 1% of the overall feeding ground sample.

Results

In the analysis of feeding grounds and nesting populations, we encountered 18 of the 23 haplotypes reported for Atlantic loggerhead turtles (Tables 1 and 2). Haplotype diversity in juvenile feeding populations was fairly uniform (*h* = 0.555–0.684) as was nucleotide diversity (*P* = 0.0221–0.0249). In both cases the lowest diversity estimates were from locations in Florida (Table 3).

The test of population structure and natal homing in juvenile turtles consisted of three classes of data analysis. The first was a comparison of haplotype distributions among 10 feeding zones along the Atlantic coast of North America, from Texas to Massachusetts. These feeding zones correspond to US states and federal management regimes, including Texas, four zones around the Florida peninsula, Georgia, South Carolina, North Carolina, the seasonal feeding habitat in Virginia, and the seasonal feeding habitat from Maryland to Massachusetts (Fig. 1). Results of AMOVA indicated that juvenile turtles were not randomly distributed among these regions: Φ_{ST} = 0.0088. This value was low on the scale of population genetic separations, but was significant in permutation tests (*P* = 0.016). When just the seven feeding grounds that are adjacent to continental nesting colonies (FL-NG, FL-SG, FL-SA, FL-NA,

**Table 3** Feeding habitat diversity estimates, including haplotype diversity (*h*) and nucleotide diversity (π)

Habitat	Haplotype diversity (*h*)	Nucleotide diversity (π)
TX	0.635 ± 0.025	0.02442 ± 0.01247
FL-NG	0.608 ± 0.086	0.02475 ± 0.01330
FL-SG	0.684 ± 0.048	0.02214 ± 0.01159
FL-SA	0.676 ± 0.024	0.02492 ± 0.01273
FL-NA	0.555 ± 0.032	0.02380 ± 0.01227
GA	0.630 ± 0.024	0.02451 ± 0.01251
SC	0.622 ± 0.035	0.02414 ± 0.01238
NC	0.576 ± 0.021	0.02337 ± 0.01193
VA	0.563 ± 0.020	0.02339 ± 0.01194
NE-US	0.579 ± 0.028	0.02355 ± 0.01205

Abbreviations are listed in Tables 1 and 2.

Fig. 2 Relationship between the frequency of haplotype CC-A1 in seven juvenile feeding areas and seven adjacent nesting beaches. The resulting correlation ($R^2 = 0.88$) was significant at $P = 0.049$.

GA, SC, NC in Table 2) were compared, the corresponding values were somewhat higher: $\Phi_{ST} = 0.0164$ ($P < 0.006$). The same comparison with conventional *F*-statistics (which do not include the divergence between haplotypes) yielded a lower but significant value ($F_{ST} = 0.0070$; $P = 0.035$). Hence our first conclusion is that juvenile loggerhead turtles are not distributed randomly among feeding habitats.

Our second approach was an assessment of haplotype frequencies at nesting populations compared to adjacent (juvenile) feeding populations. The frequency of the most common haplotype (CC-A1) at the seven nesting populations was significantly correlated with the frequencies at the seven adjacent feeding populations ($R^2 = 0.88$, $P = 0.049$; Fig. 2). Given that our data matrices included only seven values, the significant outcome was especially compelling. A Mantel test of genetic distances (Φ_{ST} values) among the seven nesting colonies (*X*-matrix) vs. genetic distances among seven feeding populations (*Y*-matrix) produced highly significant results ($R^2 = 0.52$, $P = 0.001$). Approximately half of the genetic divergence among juvenile feeding populations is correlated to genetic divergence among corresponding nesting populations. These two correlation tests provided strong support for our second conclusion, that haplotype distributions in juvenile feeding populations are significantly influenced by the composition of nearby nesting populations.

Third, the results of the Bayesian mixed stock analysis showed that nesting populations did indeed contribute more to neighbouring mixed stocks than to distant mixed stocks (Tables 4 and 5). For most rookeries, the data were too sparse to determine the destinations of neritic juveniles with certainty. The mean and median estimates of the fraction going to any one of the three (lumped) mixed stocks were close to proportional to the number of foraging grounds included in the mixed stock: 0.55 = 6/11 for
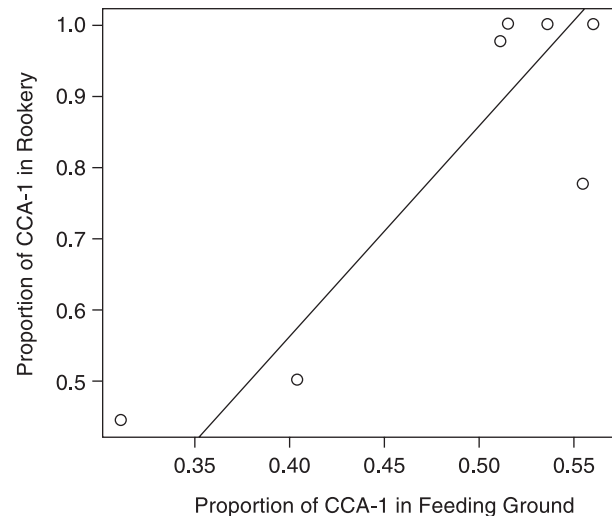
Northern, 0.09 = 1/11 for Southern, and 0.27 = 3/11 for Gulf (the denominator of 11 includes 10 feeding populations plus the 'other' category, not shown). Furthermore, the 2.5 and 97.5 percentiles of the posterior contribution for many of the stocks ranged from nearly zero to a proportional contribution above 0.5. In fact, none of the rookeries alone showed 'significantly' disproportionate contributions to the closest lumped mixed stocks, where we define significance as a 2.5 percentile of the relative contribution greater than 0.55, 0.09, or 0.27, respectively (according to the partitioning discussed above). Nevertheless, there were patterns in the results: the NEFL-NC appeared to contribute disproportionately to the Northern mixed stock (median 0.77, 2.5 percentile 0.498, null expectation 0.55), and South Florida contributed slightly more to the Gulf mixed stock (median 0.33, 2.5 percentile 0.13, null 0.25). In the disaggregated results (treating each feeding area separately; data not shown), structure was reflected in slightly enhanced contributions (> 10% over an expected proportional contribution of 9.1%) from South Florida to TX, FL-SG, GA and VA; from Mexico to FL-NG, FL-SA and SC; and from NEFL-NC to NC, VA and NE-US (see Tables 1 and 2 for abbreviations).

Looking at the results in a more traditional way, as the fraction of each feeding ground population contributed by specific rookeries (Table 5), the estimated contributions were (as expected) dominated by the size of the contributing rookeries: the three aggregate feeding-ground populations were estimated to have 82–90% contributions from the large rookery in south Florida. The main conclusion to draw from Table 5 is the very small contribution of rookeries

Table 4 Results of mixed stock analysis: proportions from each rookery contributed to specified feeding grounds

Rookery	Feeding ground	Mean	SD	2.50 percentile	Median	97.50 percentile
FL-NG	North	0.6202	0.1449	0.3209	0.6302	0.8707
	South	0.08726	0.07969	0.002518	0.06432	0.2973
	Gulf	0.2926	0.1376	0.07244	0.2769	0.5909
SFL	North	0.6058	0.1203	0.3674	0.6105	0.8255
	South	0.0555	0.03944	0.01028	0.04559	0.1596
	Gulf	0.3387	0.118	0.129	0.3322	0.578
MX	North	0.4828	0.1223	0.2498	0.4827	0.7207
	South	0.2091	0.1019	0.05463	0. 1943	0.4441
	Gulf	0.3081	0.1148	0.1127	0.3001	0.5535
NEFL-NC	North	0.7514	0.1114	0.498	0.7653	0.9262
	South	0.02831	0.0299	7.40×10^{-4}	0.01916	0.1077
	Gulf	0.2203	0.1095	0.05372	0.205	0.4723
DT	North	0.5988	0.1463	0.3026	0.6049	0.8596
	South	0.1032	0.09249	0.002652	0.07686	0.3451
	Gulf	0.298	0.1368	0.07421	0.284	0.5925
GR	North	0.5985	0.1477	0.2962	0.6051	0.8621
	South	0.09958	0.08974	0.002792	0.07463	0.3336
	Gulf	0.3019	0.1386	0.07637	0.2885	0.603
BR	North	0.6071	0.1464	0.3076	0.6147	0.8666
	South	0.08453	0.08125	0.002017	0.05967	0.3047
	Gulf	0.3083	0.1399	0.07803	0.2952	0.6105
TR	North	0.5934	0.1484	0.2947	0.5998	0.8611
	South	0.1009	0.09136	0.002971	0.07512	0.3409
	Gulf	0.3057	0.139	0.07793	0.2921	0.6066

Abbreviations: FL-NG, northwest Florida; SFL, south Florida; NEFL-NC, northeast Florida to North Carolina; DT, Dry Tortugas; MX, Mexico; BR, Brazil; GR, Greece; TR, Turkey.

outside the northwest Atlantic (Greece, Brazil, and Turkey). Despite their non-negligible size, we showed that these rookeries provided at most (95% confidence limit) about 1% of the turtles in our focal mixed stocks. (Since Table 4 shows the partitioning among mixed stocks of the total contribution to northwest Atlantic feeding habitats, it cannot provide this information).

The nesting colonies designated here as source populations represent most (but not all) of the known nesting effort in the Atlantic–Mediterranean system (Ehrhart *et al.* 2003; Margaritoulis *et al.* 2003). Important nesting efforts occur in Cuba, Cape Verde Islands, and along the coast of Africa, but could not be included for a variety of logistical reasons. Furthermore, additional nesting colonies may await discovery in undersurveyed regions. It is important to remember these limitations when formulating an interpretation of mixed stock analyses. However, more than 99% of the haplotypes observed in juvenile populations (excepting CC-A18, CC-A19, CC-A22, CC-A23; $n = 4$) could be matched to haplotypes in nesting populations, providing at least a qualitative assurance that most of the genetic diversity was captured in the existing rookery samples.

Discussion

Previous investigations have revealed that loggerhead turtles may cross entire ocean basins during their posthatchling phase (Bowen *et al.* 1995; Bolten *et al.* 1998; Resendiz *et al.* 1998; Nichols *et al.* 2000; Alfaro-Shigueto *et al.* 2004). Juveniles from nesting beaches in the northwest Atlantic inhabit oceanic zones around the Azores, Madeira, Grand Banks (Newfoundland, Canada), off the coast of Africa, and throughout the Mediterranean Sea (Bolten 2003a). Laurent *et al.* (1998) demonstrated that about half of the oceanic-stage juveniles in the Mediterranean originated on beaches of the western Atlantic. At the same time, the older neritic-stage turtles in the Mediterranean included little or no contribution from the western Atlantic (Laurent *et al.* 1998). In other words, by the time these Atlantic loggerheads switch from pelagic to neritic feeding, they have departed the Mediterranean and reappear in continental shelf habitats on the other side of the Atlantic. Notably, the switch from oceanic to neritic stages is not immutable, as both older juveniles and adults can return to oceanic habitats (Eckert & Martins 1989; Hatase *et al.* 2002b; Witzell 2002; Bolten 2003a).

Table 5 Results of mixed stock analysis: proportions of each feeding ground contributed by specified rookeries

Feeding ground	Rookery	Mean	SD	2.50 percentile	Median	97.50 percentile
North	FL-NG	0.008292	0.002842	0.003652	0.00797	0.0148
	SFL	0.8645	0.03129	0.7909	0.8687	0.9139
	MX	0.01947	0.006148	0.009428	0.01882	0.03353
	NEFL-NC	0.1018	0.02579	0.0592	0.0989	0.1614
	DT	0.002898	0.00101	0.001259	0.00279	0.005179
	GR	0.001555	0.00155	7.91×10^{-5}	0.001094	0.005711
	BR	9.80×10^{-4}	8.82×10^{-4}	5.57×10^{-5}	7.34×10^{-4}	0.003294
	TR	5.70×10^{-4}	5.54×10^{-4}	3.11×10^{-5}	4.11×10^{-4}	0.002044
South	FL-NG	0.01674	0.01959	3.61×10^{-4}	0.01038	0.07155
	SFL	0.8215	0.07938	0.6262	0.8352	0.9367
	MX	0.103	0.04618	0.03393	0.09557	0.2122
	NEFL-NC	0.0442	0.03909	0.001333	0.03336	0.1458
	DT	0.007729	0.01019	1.31×10^{-4}	0.004337	0.03522
	GR	0.003635	0.00636	2.71×10^{-5}	0.001512	0.02036
	BR	0.001733	0.002521	1.51×10^{-5}	8.27×10^{-4}	0.008925
	TR	0.001478	0.002754	9.97×10^{-6}	5.64×10^{-4}	0.008591
Gulf	FL-NG	0.008005	0.005311	0.001609	0.00677	0.02194
	SFL	0.9022	0.04311	0.7959	0.9104	0.9611
	MX	0.02521	0.0133	0.007518	0.02252	0.05865
	NEFL-NC	0.05827	0.03239	0.01363	0.05253	0.1372
	DT	0.002963	0.001972	5.90×10^{-4}	0.002512	0.007989
	GR	0.00165	0.002143	5.66×10^{-5}	9.87×10^{-4}	0.007048
	BR	0.001119	0.001428	3.48×10^{-5}	6.51×10^{-4}	0.005034
	TR	6.29×10^{-4}	8.21×10^{-4}	2.08×10^{-5}	3.76×10^{-4}	0.002792

NEFL-NC is a category combining nesting beaches from northeast Florida, Georgia, South Carolina and North Carolina. Other abbreviations are described in Tables 1–4.

Three analyses were conducted to test for population subdivisions and natal homing behaviour in juvenile loggerhead turtles of the northwest Atlantic: (i) an AMOVA for juvenile feeding populations ($\Phi_{ST} = 0.0088$; $P = 0.016$); (ii) correlation statistics to compare genotype frequency differences in nesting populations vs. adjacent feeding populations (Mantel $R^2 = 0.52$; $P = 0.001$), and (iii) a mixed stock analysis using Bayesian methodology. All three approaches indicate a nonrandom distribution of juvenile turtles, and a significant relationship between nesting colonies and adjacent feeding populations. Collectively these analyses yield substantial evidence of natal homing in developmental migrations. Tagging studies, indicating high site fidelity in juvenile turtles on the Atlantic coast, indirectly support this conclusion (Avens *et al*. 2003; Hopkins-Murphy *et al*. 2003).

One caveat to these conclusions is that the correlation statistics are based on a subset of the entire database, specifically the seven nesting locations along the continental coastline of the southeastern USA (Table 1), and their adjacent feeding populations (Table 2). A second caveat is that sampled individuals may have included a few small adults, and certainly included a wide range of juvenile age classes, from new neritic-stage recruits to older turtles approaching maturity. A third qualification is that we have not sampled the entire range of feeding habitat in the northwest Atlantic (see Engstrom *et al*. 2002). Given these limitations, we caution that the affinity described here between nesting colonies and adjacent juvenile feeding areas does not verifiably extend beyond the continental shelf of North America.

Population structure and life history implications

Subsequent to the oceanic juvenile stage, loggerhead turtles switch to primarily neritic, benthic foraging habitats. These neritic foraging habitats may be a great distance from the oceanic habitats, from Baja California to Japan, for example, or from the Azores to the eastern coast of North America. Whereas the migration to oceanic feeding areas is apparently facilitated by passive drift, the return trip may include active swimming. Once juveniles return to their region of origin and switch to benthic feeding, they may occasionally return to a pelagic feeding mode, as indicated by satellite telemetry, stable isotope ratios and tag returns (Eckert & Martins 1989; Hatase *et al*. 2002b). Juvenile turtles make

seasonal migrations into temperate habitats (such as the northeast US coast), and adults make reproductive migrations over hundreds of kilometres (Limpus *et al.* 1992; Schroeder *et al.* 2003). We conclude that the complex life history of loggerhead turtles may include two homing migrations. The first is a migration from oceanic habitat (often thousands of kilometres from the nesting beach) to the region of origin. The second is the cyclic reproductive migration from adult foraging habitat to courting grounds and nesting habitat.

Our analyses demonstrate that there is genetic structure among feeding ground populations and that this genetic structure is spatially correlated with the genetic structure of nesting populations. The technique that comes closest to answering our specific question—how the contribution of rookeries to foraging grounds is partitioned—results in wide confidence intervals, but with some consistent trends. First, there is little contribution from assayed nesting colonies outside the northwest Atlantic (the parameter giving relative contributions from outside the northwest Atlantic has a mean of 0.03, with an upper confidence limit of 0.11). Second, there are indications (supporting our simpler analyses of correlation in frequency of the dominant haplotype) of targeted contributions from rookeries to nearby feeding grounds, especially from the south Florida rookery to foraging grounds in the Gulf of Mexico and from Atlantic rookeries (NEFL-NC) to Atlantic foraging habitats. However, no rookery–foraging ground pair actually shows significantly greater contributions than a proportional null model. Mixed stock analyses do not allow strong conclusions at this level of resolution. While this limitation can partly be overcome with more data, some of it is inherent in the overlap of haplotype profiles among rookeries and foraging grounds. We are working to incorporate spatial structure into the framework of mixed stock analysis, so that we can more powerfully test specific spatial hypotheses (Bolker *et al.* unpublished results).

Marine turtles have a complex population structure, with lower levels of population differentiation in nuclear DNA assays relative to mtDNA assays (Karl *et al.* 1992; FitzSimmons *et al.* 1996, 1997b; Pearce 2001; Roberts *et al.* 2004). Superimposed on this pattern are the life history stages of loggerhead turtles, with varying degrees of population structure. Oceanic juveniles are well mixed in the North Atlantic (Bolten *et al.* 1998; LaCasella *et al.* 2004; P. Dutton unpublished data); the neritic juveniles of the western Atlantic subsequently segregate at a low but significant level ($\Phi_{ST} = 0.0088$; $P = 0.016$); and corresponding nesting populations are highly structured ($\Phi_{ST} = 0.27$; $P < 0.001$ for the seven rookeries compared to adjacent feeding cohorts).

In this study we consider two primary influences on the distribution of neritic-stage juveniles: the size of the source populations and the proximity of juvenile feeding habitat to these source populations. However, additional factors will certainly influence the distribution of juveniles. Hopkins-Murphy *et al.* (2003) demonstrate that larger juveniles dominate the feeding habitat in the eastern Gulf of Mexico (FL-NG and FL-SG), while smaller juveniles are more prevalent in the peripheral and seasonal habitats of the western Gulf of Mexico (TX) and the northeast USA. Analyses of haplotype distributions among size classes may prove fruitful in teasing apart these additional life-history components.

Notably, one life stage in North Atlantic loggerheads remains to be evaluated with mtDNA surveys: the adult feeding populations. Little is known about adult feeding habitats, but (for loggerheads nesting in the southeast USA) they include sites along the east coast of the USA, the Bahamas, Cuba, Gulf of Mexico and Caribbean Mexico (Hopkins-Murphy *et al.* 2003; Schroeder *et al.* 2003). It will be informative to survey the adult cohorts and determine whether they also segregate on feeding grounds. It would also be informative to test the juvenile homing hypothesis in other regions (Mediterranean Sea, Japan), and in other sea turtle species.

Conservation implications

The finding of significant population structure in juvenile loggerhead turtles carries some implications for wildlife management. The hazards that affect breeding populations may also have an impact on the next generation that is feeding in nearby waters. However, homing is not absolute and considerable movement occurs as well. The stranding data from Texas and the northeast USA, where nesting is sparse or absent, illustrate that feeding populations extend far past the regional nesting habitat (Fig. 1). One consequence of this widespread foraging is that juvenile turtles originating in Yucatan Mexico are feeding in US waters (Table 5). We suspect the converse is true (Table 4). This finding invokes the provisions of the 1982 United Nations Convention on the Law of the Sea, in which nations that host the developmental habitat for migratory marine species hold fishing rights for these animals on the high seas (Van Dyke 1993). The 1983 UN Convention on the Conservation of Migratory Species (also know as the Bonn Convention) prohibits taking endangered species during migrations on the high seas (Hykle 1992). Under the principles outlined in these international agreements, nations that host nesting and developmental habitats for marine turtles have some level of jurisdiction over these animals on geographically remote feeding grounds, even if those feeding grounds are within the territorial boundaries of another nation. Activities in US waters can deplete an embattled rookery in Mexico, and activities in Mexico could have an impact on threatened nesting populations in the southeastern USA. Provisions of international law apply here.

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